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Ego C, Orban de Xivry JJ, Nassogne MC, Yüksel D, Lefèvre P. The saccadic system does not compensate for the immaturity of the smooth pursuit system during visual tracking in children. *J Neurophysiol* 110: 358–367, 2013. First published April 24, 2013; doi:10.1152/jn.00981.2012.—Motor skills improve with age from childhood into adulthood, and this improvement is reflected in the performance of smooth pursuit eye movements. In contrast, the saccadic system becomes mature earlier than the smooth pursuit system. Therefore, the present study investigates whether the early mature saccadic system compensates for the lower pursuit performance during childhood. To answer this question, horizontal eye movements were recorded in 58 children (ages 5–16 yr) and 16 adults (ages 23–36 yr) in a task that required the combination of smooth pursuit and saccadic eye movements. Smooth pursuit performance improved with age. However, children had larger average position error during target tracking compared with adults, but they did not execute more saccades to compensate for their low pursuit performance despite the early maturity of their saccadic system. This absence of error correction suggests that children have a lower sensitivity to visual errors compared with adults. This reduced sensitivity might stem from poor internal models and longer processing time in young children.

eye movements; brain maturation; internal model; cerebellum; development

FROM BIRTH TO ADULTHOOD, the brain changes through experience (Toga et al. 2006). For instance, the number of synapses increases until adolescence (~12 yr) and then decreases because of synaptic pruning (Giedd et al. 1999; Gogtay et al. 2004). These changes in brain structure are accompanied by improvements of cognitive and motor functions. For instance, the speed of walking adaptation increases with age (Vasudevan et al. 2011). Similarly, the ability to reach and grasp objects improves through a better ability of the central nervous system to estimate the state (position, velocity, and acceleration) of the arm (King et al. 2012). Given their lower ability for state estimation, young children preferentially rely on visual feedback in order to achieve motor tasks (Rösblad 1997). This strategy allows them to compensate for their immature reaching behavior. Such a compensation strategy is at the heart of the present study.

The saccadic and smooth pursuit systems follow very different developmental time courses. The saccadic system becomes mature early in life. Saccade kinematics in children is comparable to adults at ~6 yr. For instance, saccadic peak velocity is similar or slightly higher in children than in adults, and the accuracy in children's saccades does not suffer from the increase in peak velocity (Accardo et al. 1992; Irving et al. 2006; Salman et al. 2006a). This surprising high speed has been related to higher reward sensitivity in children (Shadmehr et al. 2010a). However, saccade latency and its variability decrease with age during childhood (Fukushima et al. 2000; Klein 2001; Klein et al. 2011; Salman et al. 2006a), indicating that the motor component is mature very early in development while the saccade latency decreases until 12–15 yr (Fukushima et al. 2000; Irving et al. 2006; Luna et al. 2004).

In contrast, the developmental time course of the smooth pursuit system is much slower. The smooth pursuit system continuously improves until late adolescence (Rütsche et al. 2006; Salman et al. 2006b; Von Hofsten and Rosander 1997). In most studies, the use of predictable stimuli assessed the predictive abilities of children and their visually guided pursuit abilities together. In such circumstances, pursuit phase lag decreases and pursuit gain increases with age and becomes close to reported adult values by middle or late adolescence, between 13 and 18 yr (Accardo et al. 1995; Katsanis et al. 1998; Salman et al. 2006b) or earlier (~6–7 yr) for lower target velocities (Ross et al. 1993; see Luna et al. 2008 for review). For instance, for a target moving sinusoidally (at ±10° amplitude and 0.25 Hz), pursuit gain, defined as the ratio of the eye to the target velocity, increases from ~0.7 at 8 yr to ~1 at 19 yr (Salman et al. 2006b). In contrast, very few studies have focused on pursuit initiation and on unpredictable target motion. Pursuit initiation provides information about the ability to process sensory errors (i.e., retinal slip) required to initiate smooth pursuit eye movements. Unpredictable target velocity avoids the influence of predictive mechanisms. A study that used low unpredictable target velocities found no changes in pursuit initiation with age despite lower pursuit gains (Ross et al. 1994).

In adults, low pursuit gains are often compensated by catch-up saccades in order to align the projection of the target with the fovea on the retina. The amplitude of these catch-up saccades is based on an estimate of future position error computed from position and velocity errors (de Brouwer et al. 2002a). Similarly, during transient target disappearance, saccades are used to compensate for the decrease in smooth pursuit velocity in order to minimize position error at target reappearance (Orban de Xivry et al. 2006). Even children use saccades to compensate for a low pursuit gain. Indeed, during visually guided smooth pursuit, saccadic and smooth eye displacements of chil-

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dren aged 7–18 yr were inversely correlated (Katsanis et al. 1998; Ross et al. 1993). It is, however, unknown whether this compensation improves with age.

The present study aims at investigating the developmental time course of the smooth pursuit system with a minimized influence of the predictive mechanisms. In addition, it focuses on the compensation strategy. That is, does the early mature saccadic system compensate for the immaturity of the smooth pursuit system during childhood?

METHODS

Participants. Eye movements were recorded in a total of 74 subjects, including 58 children aged 5–16 yr who were divided into four groups and 16 adults (Table 1). None of the subjects had any oculomotor disabilities. After a complete description of the procedure, written consent was obtained either directly from all subjects or from their parents if they were under 18. All procedures were approved by the Université catholique de Louvain Ethics Committee and were in accordance with the Declaration of Helsinki.

Experimental setup. Subjects were seated on a chair placed 1.5 m away from a screen (195 × 145 cm) where the target was projected by a cine8 Barco projector (refresh rate: 100 Hz; Barco). Head movements were limited by using a forehead and chin rest. Horizontal eye movements of the left eye of each participant were recorded with an Eyelink 1000 infrared eye tracker (SR Research, Ottawa, ON, Canada) at 1,000 Hz.

Paradigm. Each trial consisted of a double step-ramp stimulus (de Brouwer et al. 2002a) (Fig. 1*A*). A fixation target (1° green dot) was presented for 1 s on one side of the screen (randomly from 22° to 12° to the left or to the right of the screen center). The target then stepped 3° away from the center of the screen and started moving toward the center at 15°/s for 600, 700, or 800 ms (Rashbass 1961) (1st ramp, Fig. 1*A*). After the end of the first ramp, the target stepped again and continued moving with a different velocity (2nd ramp, Fig. 1*A*). The position step (PS) was randomly chosen between −10°, 0°, or 10°, and the velocity step (VS) between ±45°/s, ±30°/s, and ±15°/s. During the second ramp, the target was therefore moving at a velocity ranging from −30°/s to 60°/s for 600–800 ms. Each trial consisted of a combination of one PS and one VS as described in Fig. 1*B*. For instance, a trial with a negative PS (−10°) and a VS of 45°/s (leading to a second ramp at 60°/s) was abbreviated as PS −10 VS 45. The randomization of the initial position and ramp durations was restricted to keep the target in the range between ±25°. For the same reason, the duration of the first ramp was restricted to 500 ms for the conditions PS 10 VS 45 and PS −10 VS −45. At the end of the second ramp, the target stopped and became red, indicating the end of the trial. Subjects were instructed to track the target with their eyes as accurately as possible. Each subject completed between 10 and 18 blocks of 18 trials corresponding to the 18 different combinations of PS and VS that were randomly shuffled within each block.

The oculomotor behavior was quite different depending on the combination of PS and VS. The conditions with PS and VS of opposite signs are very similar to a Rashbass paradigm. Similarly to a previous study (de Brouwer et al. 2002b), we found that in these

Table 1. *Number of subjects per age group*

Group	Age, yr	*n*
1	5–7	15
2	8–9	15
3	10–11	14
4	12–16	14
5	23–36	16

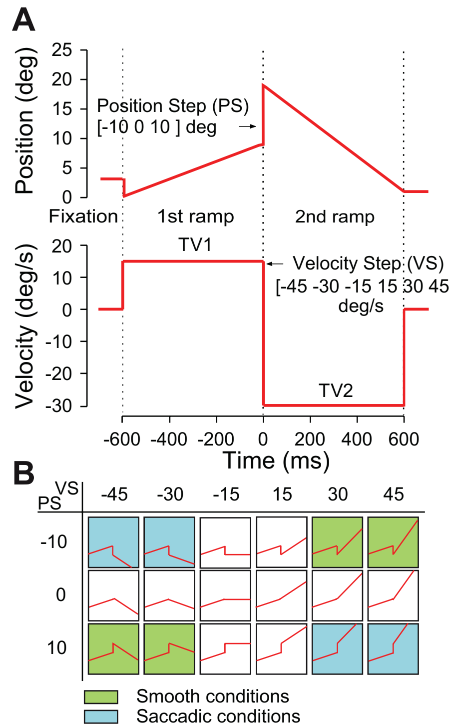

Fig. 1. *A*: typical stimulus for the double step ramp paradigm. The position of the target as a function of time is represented at *top*, while the velocity is represented at *bottom*. Each trial begins with a fixation period of 1 s followed by a small step in the direction opposite to the future target motion at constant velocity (TV1 = 15°/s). After a random period, the target stepped again (position step, PS) and continued moving at a different velocity (velocity step, VS). *B*: among the 18 different combinations of PS and VS, some conditions called smooth conditions are mainly used to study the smooth pursuit. Others that always lead to the execution of a saccade after the step are called saccadic conditions and are used to study the saccadic response.

conditions, since after the second step the target crossed the current position of the eye, smooth eye movements could be sufficient to catch the target. Among these conditions, the four conditions with the highest proportion of trials without any saccade after the second step were called smooth conditions (PS −10 VS 30 or 45 and PS 10 VS −30 or −45) (Fig. 1*B* and example in Fig. 2). In contrast, when PS and VS have the same sign, saccades are always observed in response to the second step. Four of these combinations (PS 10 VS 30 or 45 and PS −10 VS −30 or −45) were called saccadic conditions (Fig. 1*B*). The percentage of trials with at least one saccade in the first 300 ms after the second step is 98% in the saccadic conditions versus 41% in the smooth conditions.

Data analysis. Position signals were low-pass filtered at 50 Hz with a bidirectional autoregressive zero-phase filter implemented in MATLAB (de Brouwer et al. 2001). Velocity and acceleration signals were obtained from position with a central difference algorithm on a 20-ms window.

Saccades were detected based on an acceleration criterion of 500°/s^2 and a minimum duration of 30 ms and were removed from the velocity traces to analyze the smooth pursuit response. Saccades were replaced by a linear interpolation between the velocity before and after the saccades.

Pursuit performance was examined on the first ramp for all trials and on the second ramp for the trials corresponding to the smooth conditions. The analyzed parameters were the onset, the initial acceleration, and the gain of the smooth pursuit.

Pursuit onset and acceleration were determined by fitting a piecewise linear function on the eye velocity trace:

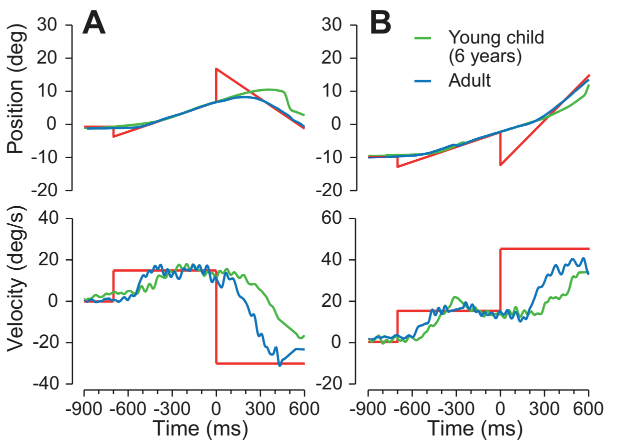

Fig. 2. Typical pursuit response during a single trial of 1 of the youngest children compared with 1 adult. *Top*: position vs. time. *Bottom*: desaccaded velocity vs. time. Red traces represent target motion. These 2 trials were taken from the smooth conditions with PS and VS of opposite sign (*A*: PS 10 VS −45; *B*: PS −10 VS 30).

$$f(t) = \begin{cases} V & \text{if } t < t_0 \\ A(t - t_0) & \text{if } t \geq t_0 \end{cases}$$

where V is the initial eye velocity (°/s) before pursuit onset and A is the initial eye acceleration (°/s^2). A, V, and t_0 were the parameters of the fit. For the first ramp, this function was fitted on the velocity trace on the first 250 ms after the stimulus onset. For the second ramp, the time at which the eye velocity deviated from more than two times the standard deviation around the initial velocity at the step gave a first approximation of the onset. Then pursuit onset and acceleration were determined by fitting the same function on an interval starting 100 ms before the step until 150 ms after the previously estimated onset to refine the measurement. Trials with saccades or position error > 5° during the fitting time interval were removed for the analyses of the first ramp (25% of trials). Trials with position error > 2° just before the step or anticipatory pursuit (onsets before the step) were removed for the analyses of the second ramp (24% of trials).

The gain was defined as the ratio between the mean eye velocity between 450 and 550 ms after first or second ramp onset and target velocity. For this analysis, trials with position error > 5° (for the first ramp 2% of trials) or mean position error > 5° (for the second ramp 14% of trials) during this time interval were excluded.

The latency of the first saccade after the second step was studied in trials from the saccadic conditions (as defined above; Fig. 1*B*). For this analysis, trials with position error < 2° before the step and with no saccades in an interval starting 50 ms before until 50 ms after the step were analyzed (24% of trials excluded).

The average position error during the first ramp was measured as the integral of the absolute value of the position error between 300 and 600 ms after the first ramp onset divided by the duration of this time interval. For this analysis, all trials with position error > 5° during this time interval were removed (6% of trials).

For each of these analyses, the mean was computed for each subject individually and plotted as a function of age. For the analyses conducted on the second ramp, the tendencies were the same across the four conditions (smooth or saccadic; Fig. 1). Therefore, data from the different conditions were collapsed together. Linear regressions were used to assess the evolution of these parameters with age during childhood. In addition, the evolution of these parameters was studied over the course of the different blocks of trials in order to assess the possible differences in attention/fatigue between children and adults.

Repeated-measures ANOVA with condition as within-subject factors and age group as between-subject factor and the P value for the slope of the regression line were used as markers of developmental changes. The confidence interval for the mean adult value was compared to the confidence interval of the linear regression to assess the maturity threshold. The age at which those confidence intervals overlap was considered the maturity threshold.

The effect of fatigue or decrease in attention can be reflected in the evolution of pursuit or saccade parameters in the course of the experiment. Trials from each subject were divided into three time periods. Repeated-measure ANOVA with time period and age group as factors were used to assess the possible evolution of the pursuit and saccade parameters.

Regardless of the condition, trials without any saccades in the first 300 ms after the second step were called smooth trials since the eye only used the smooth pursuit system to catch the target. The other trials (with at least 1 saccade in the time interval from the second step to 300 ms after the step) were called saccadic trials.

To study saccadic programming, we used the eye crossing time (T_{XE}) as defined by de Brouwer et al. (2002b). T_{XE} is defined as the time period it would take for the eye trajectory to cross the target if the eye continued moving at the same velocity ($T_{XE} = -PE/RS$, where PE is position error and RS is retinal slip). Data from all 18 different conditions were used for this analysis. Trials were classified in the two categories described above: trials with at least one saccade in the first 300 ms after the step (saccadic trials) and trials without any saccade in this time interval (smooth trials). For saccadic trials, the value of T_{XE} that triggered the saccade was computed with the position error and the retinal slip 75 ms before saccade onset. Trials with a first saccade with latency shorter than 75 ms were excluded for this analysis since their programming could be based on visual information before the step. For smooth trials, T_{XE} was the average T_{XE} over the first 300 ms after the step. T_{XE} was computed for each trial classified as smooth or saccadic. The proportion of saccadic trials was reported for each T_{XE} by pooling the data from all subjects from the same age group. The smooth zone was defined as the range of T_{XE} for which the probability of observing a saccade (% of saccadic trial) is lower than 50% and represents all the combinations of position error and retinal slip that did not trigger a saccade. A permutation test was used to test the significance of the difference in the smooth zone duration between the adults and the other age groups (Moore et al. 2009).

All trials with blinks were removed from all analyses (5% of trials).

RESULTS

In this experiment, smooth pursuit is studied in two situations: in a first ramp at moderate (15°/s) constant velocity (starting from fixation) and then in reaction to a sudden change in position and velocity of the target (during ongoing pursuit). Typical oculomotor responses from one of the youngest children and one adult are displayed in Fig. 2. After an initial period of fixation, both the child and the adult reacted to this moving target with a typical

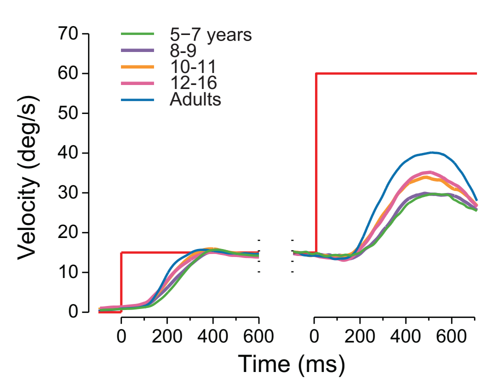

Fig. 3. Intersubject average velocity profile for the different age groups on all the trials (1st ramp on *left*) and for all trials with a −10° PS and a 45°/s VS (2nd ramp on *right*).

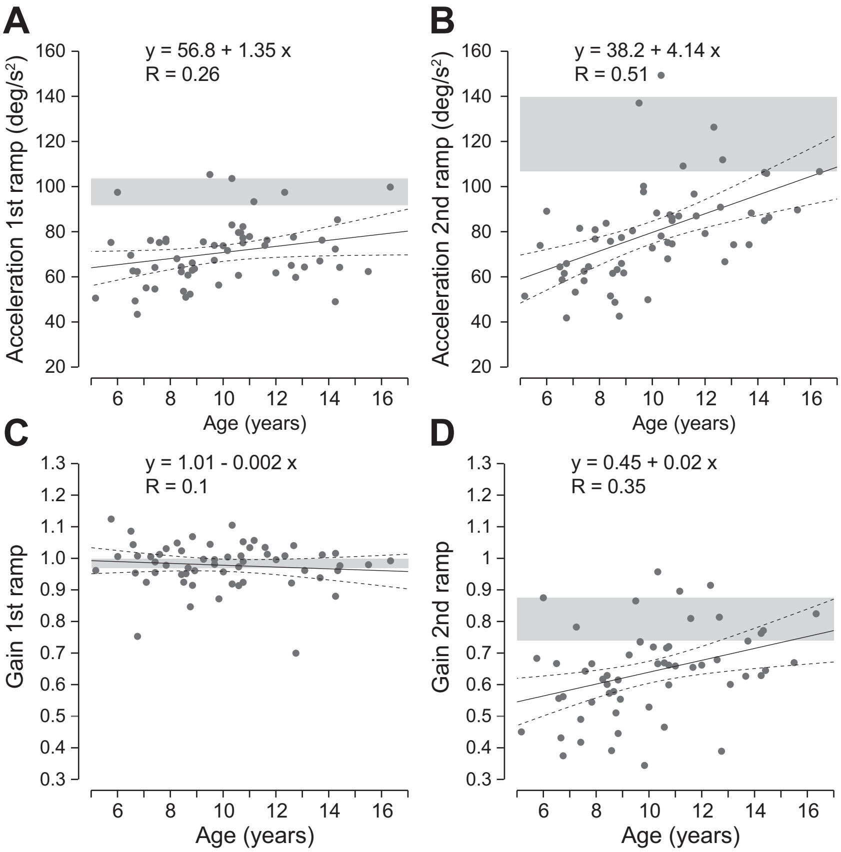

Fig. 4. Evolution with age of pursuit acceleration (*A* and *B*) and gain (*C* and *D*): pursuit of the first ramp at 15°/s (*A* and *C*) and pursuit response to the PS and VS (*B* and *D*). For all panels, each dot represents the mean for 1 subject. In *B* and *D* dots are the mean by subject across the 4 smooth conditions. Regression lines fitted on the means by subject characterize the evolution with age during childhood. The gray zone represents the confidence interval for the adult group.

smooth pursuit response, but the adult reacted sooner and accelerated faster during the initiation of pursuit. However, for this first ramp, both subjects reached target velocity. The target position and velocity then suddenly stepped. Again, both subjects reacted to this change of target motion and modified their pursuit response, but the adult reacted sooner and faster than the child. In addition, the child's eye velocity remained lower than the adult's velocity during this second ramp. These typical trials suggest that there are major differences between the smooth pursuit response of adults and children, which is investigated further below.

Smooth pursuit gain, initial acceleration, and latency evolve with age. The subjects were categorized into five age groups, and the average smooth pursuit response for each of these categories is presented in Fig. 3. These average trials were obtained from all trials for the first ramp (Fig. 3, *left*) and from the trials of one of the smooth conditions for the second ramp. The age group largely influences these velocity profiles, with initial acceleration increasing with age for both the first and second ramps. However, peak eye velocity appeared similar across age groups for the first ramp but not for the second ramp.

Most parameters of the smooth pursuit improve with age and become mature during childhood or during late adolescence (Fig. 4). The initial eye acceleration during the first ramp slightly increases with age in children from 5 to 16 yr old (Fig. 4*A*; $P = 0.05$). However, the acceleration value of the oldest children of the study does not reach adult levels [no overlap between the confidence interval of the regression and the confidence interval of adults (Fig. 4)]. Similarly, pursuit accel-

Table 2. *Statistics on smooth pursuit and saccadic performances*

Parameters	Slope of Regression Line	Significance of Regression Line	Age of Maturity, yr	Main Effects and Interactions: Age	PS	VS
Onset	−4.3 ms/yr	$P = 0.003$	8–9	**$F(4,69) = 3.583$, $P = 0.01$**	**$F(1,69) = 319.61$, $P < 0.001$**	**$F(1,69) = 6.39$, $P = 0.014$**
SD onset	−1.3 ms/yr	$P < 0.001$	14	**$F(4,69) = 10.09$, $P < 0.001$**	**$F(1,69) = 133.26$, $P < 0.001$**	**$F(1,69) = 18.41$, $P < 0.001$**
Acc	$4.14° \cdot s^{-2} \cdot yr^{-1}$	$P < 0.001$	14	**$F(4,69) = 15.60$, $P < 0.001$**	**$F(1,69) = 110.54$, $P < 0.001$**	**$F(1,69) = 98.66$, $P < 0.001$**
Gain	0.02/yr	$P = 0.007$	13	**$F(4,69) = 7.526$, $P < 0.001$**	**$F(1,69) = 57.31$, $P < 0.001$**	**$F(1,69) = 139.12$, $P < 0.001$**
Latency 1st saccade	−4.4 ms/yr	$P = 0.015$	12	**$F(4,69) = 5.56$, $P < 0.001$**	**$F(1,69) = 147.23$, $P < 0.001$**	**$F(1,69) = 13.69$, $P < 0.001$**
SD latency 1st saccade	−1.6 ms/yr	$P = 0.02$	14	**$F(4,69) = 9.97$, $P < 0.001$**	**$F(1,69) = 16.53$, $P < 0.001$**	$F(1,69) = 0.33$, $P = 0.57$

PS, position step; VS, velocity step; Acc, acceleration. Boldface indicates significance.

eration in response to the second VS increases with age ($P < 0.001$; Fig. 4*B*). This parameter reaches adult levels at ~14 yr of age. The VS and the PS influenced pursuit acceleration, but these influences did not differ across age groups (Table 2). The results of the statistical analyses of the effect of age, PS, and VS on smooth pursuit parameters and the corresponding age of maturity are presented in Table 2.

For all subjects, the gain of the pursuit response during the first ramp was close to unity. Therefore, it did not evolve with age (Fig. 4*C*; $P = 0.43$). Sustained pursuit of a target moving at 15°/s is therefore considered mature at 5 yr. In contrast, during the second ramp the pursuit gain is below unity and increases with age ($P = 0.007$) (Fig. 4*D*). The gain of the pursuit response after the second VS reached adult level at ~13 yr of age. This gain decreased with increasing VS and was lower for a target going in the same direction as the pursuit on the first ramp than for a target going in the opposite direction (Table 2). This effect of direction increased with age (interaction between PS and age) but was independent of the magnitude of VS (see Table 2 for statistics).

Finally, the latency of the smooth pursuit response decreases with age during both the first ($P < 0.001$) and the second ($P = 0.003$) ramps. The standard deviation of the latency also decreases with age (first ramp: $P < 0.001$; second ramp: $P < 0.001$). However, while average smooth pursuit latency reached adult value at ~8–9 yr of age, the standard deviation of this parameter remained higher than adults until 16 and 14 yr for the first and second ramps, respectively.

Age-related differences in attention or fatigue cannot explain the observed differences. Fatigue or inattention would increase pursuit latency and decrease pursuit gain or acceleration. None of those effects was found. Rather, there was an increase in pursuit acceleration and in pursuit gain over the course of the experiment (Table 2). These effects were quantified by dividing each experimental session into three periods (see METHODS). The influence of the period on the main parameters is summarized in Table 2. Therefore, practice seemed to improve performance. Importantly, these effects appeared similar for all age groups (Table 2).

Catch-up saccades are accurate but less frequent in younger children. Given the low initial acceleration and the reduced pursuit gain in children, we hypothesized that children relied on the saccadic system to track the target more closely. An increased number of saccades or shorter catch-up saccade latencies would provide evidence for this compensation strategy.

In contrast, we found that the number of catch-up saccades observed during the first 300 ms after the step in the saccadic conditions increased with age (regression lines: $P < 0.02$ for all saccadic conditions). In the smooth conditions, the number of catch-up saccades was also influenced by the age group [main effect of age group: $F(4,69) = 6.81$, $P < 0.001$]. Indeed, despite the fact that these trials were designed to reduce the probability of observing a catch-up saccade, subjects did elicit catch-up saccades in some of those trials as illustrated in Fig. 5*A*. To quantify the proportion of trials from the smooth condition with (saccadic trials) and without (smooth trials) saccades, we normalized the number of trials with a saccade during the first 300 ms after the steps by the total number of trials in these conditions for each subject separately. The percentage of saccadic trials was low for the youngest children (~25%) and was much higher in adults (~60%; Fig. 5*B*). There is a main effect of age group on the percentage of saccadic trials [$F(4,69) = 5.2941$, $P < 0.001$]. The percentage of saccadic trials is significantly different in children aged 5–7 yr compared with adults (other differences between child age groups did not reach significance). Note that this result does not depend on the length of the time interval (300 ms for Fig. 5*B*) chosen to determine the number of saccadic trials (Fig. 5*C*).

Despite the low number of saccades in children, saccades with shorter latencies could help children track the target more closely. However, the histograms of saccade latencies from the youngest children and the adults reveal that this is not the case (Fig. 6*A*). The peak of the histogram of saccade latencies is earlier for the adults. In addition, the spread of their latency distribution is also much smaller than for children. As suggested by Fig. 6*A*, the mean latency of the first saccade after the step decreases with age ($P = 0.015$; Fig. 6*B*). This latency was also influenced by the step direction. Saccades had shorter latencies when the PS was in the direction of target motion than when it was in the opposite direction (main effect of the PS, Table 2). The effect of PS decreased with age (interaction between PS and age, Table 2). As illustrated in Fig. 6*A*, the histograms of saccade latencies become narrower with age. There is a significant decrease in the variability of saccade latency with age ($P = 0.02$; Fig. 6*C*). This variability decreases to adult level for 14-yr-old children.

Despite a lower frequency of saccades and longer latencies, saccade accuracy was comparable across all age groups (all Dunnett *t*-tests are nonsignificant), although children aged 10–11 yr had a smaller position error at the end of the first saccade than adults [$t(68) = 3.92$, $P = 0.03$].

Table 2. *Continued*

Main Effects and Interactions					
Age × PS	Age × VS	PS × VS	Age × PS × VS	Period	Period × Age
$F(4,69) = 0.875$, $P = 0.48$	$F(4,69) = 0.866$, $P = 0.49$	**$F(1,69) = 20.91$, $P < 0.001$**	**$F(4,69) = 3.007$, $P = 0.024$**	$F(2,136) = 1.18$, $P = 0.31$	$F(8,136) = 0.84$, $P = 0.56$
$F(4,69) = 1.325$, $P = 0.27$	$F(4,69) = 2.40$, $P = 0.059$	**$F(1,69) = 16.073$, $P < 0.001$**	$F(4,69) = 1.337$, $P = 0.27$		
$F(4,69) = 0.08$, $P = 0.99$	$F(4,69) = 1.32$, $P = 0.27$	$F(1,69) = 0.15$, $P = 0.69$	$F(4,69) = 0.78$, $P = 0.54$	**$F(2,136) = 11.06$, $P < 0.001$**	$F(8,136) = 1.78$, $P = 0.08$
$F(4,69) = 4.537$, $P = 0.003$	$F(4,69) = 0.42$, $P = 0.79$	$F(1,69) = 0.57$, $P = 0.45$	$F(4,69) = 0.82$, $P = 0.52$	**$F(2,136) = 3.36$, $P = 0.04$**	$F(8,136) = 0.52$, $P = 0.84$
$F(4,69) = 5.49$, $P < 0.001$	$F(4,69) = 0.35$, $P = 0.84$	$F(1,69) = 0.076$, $P = 0.78$	$F(4,69) = 0.29$, $P = 0.88$	$F(2,136) = 0.36$, $P = 0.69$	$F(8,136) = 1.71$, $P = 0.10$
$F(4,69) = 1.19$, $P = 0.32$	$F(4,69) = 0.66$, $P = 0.62$	$F(1,69) = 0.70$, $P = 0.40$	$F(4,69) = 0.78$, $P = 0.78$		

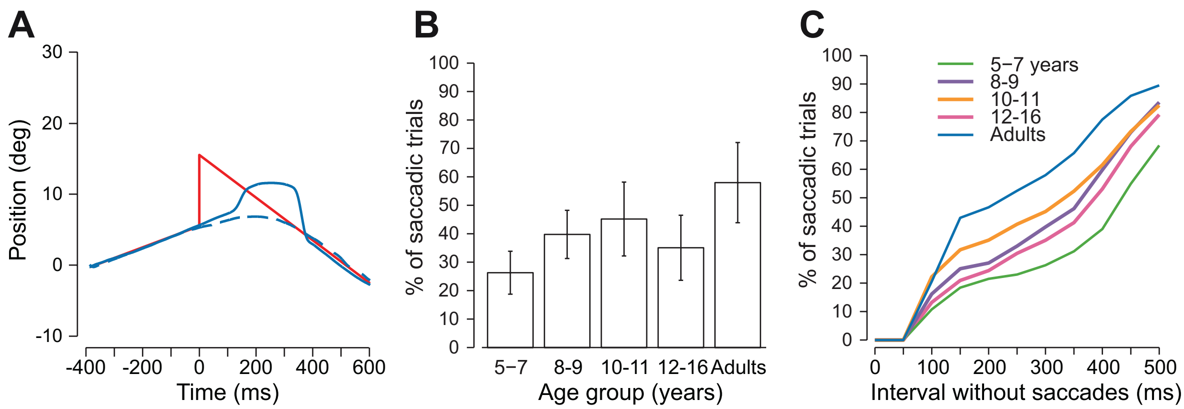

Fig. 5. *A*: position of the eye as a function of time in response to a PS of 10° and a VS of −45°/s for 2 single trials. Two behaviors can be elicited in response to the step. Either only the smooth pursuit is used, there is no saccade in the first 300 ms after the step, and trials are called smooth trials (dashed line) or the saccadic system is used and trials are called saccadic trials (solid line). *B*: mean % of saccadic trials for all smooth conditions for the different age groups increases with age. *C*: mean % of saccadic trials for the different age groups as a function of the time interval chosen to determine whether the trial is smooth or saccadic. The increased proportion of saccadic trials with age does not depend on this interval.

Absence of compensation results in lower tracking performance. Given their low pursuit performance and their low frequency of saccades, children should have a lower tracking performance. To quantify the global performance of the subjects (including the contribution of smooth pursuit and saccades), the duration during which subjects had a good vision of the target was computed. This analysis was restricted to the first 500 ms of the second ramp. Within this time period, the duration of pursuit with a position error $< 2°$ was extracted. Saccade periods were excluded from this measure (Fig. 7*A*) because of the absence of some visual information during the saccades. Pursuit durations close to the target (Fig. 7*A*) were then summed over the 500-ms interval. In smooth conditions, global tracking performance was higher in adults than in children. This measure improves with age [Fig. 7*B*; $F(4,69) = 6.267$, $P < 0.001$]. Post hoc analysis shows that this duration is higher for adults than for all children [Dunnett test: group (G)1 vs. G5: $P = 0.001$, G2 vs. G5: $P < 0.001$, G3 vs. G5: $P = 0.009$, G4 vs. G5: $P = 0.036$]. This result is valid for a wide range of thresholds (Fig. 7*C*). For small thresholds ($<3°$), the tracking performance of adults remains higher than the other age groups. The same analysis on the first ramp shows similar results (data not shown).

Children tolerate larger errors. The observation that children can elicit saccades with latencies as short as adults (Fig. 6*A*) suggests that the low frequency of catch-up saccades is not due to motor inabilities. In addition, despite adultlike pursuit gains, children have, on average, larger position error during the first ramp (measured from 300 ms to 600 ms). This average position error during sustained pursuit decreases with age (Fig. 8; $P = 0.002$) and becomes mature at ~13 yr of age. This analysis suggests that despite good pursuit gain and the ability to trigger short-latency accurate catch-up saccades, children tolerate larger average position errors. Therefore, the mechanisms of saccade trigger should differ between children and adults.

To investigate saccade trigger, we compared the sensory conditions leading to the execution of a saccade in children and adults. This sensory condition can be quantified by T_{XE}, which is the opposite of the ratio between position error and retinal slip and has units of time (s). This parameter defines the time at which the eye trajectory would cross the target trajectory given constant eye velocity.

T_{XE} was computed for each trial. In trials with a saccade in the first 300 ms after the step, position and velocity errors were measured 75 ms before the saccade. In trials without a saccade in the first 300 ms, the average position and velocity errors were computed over the first 300 ms after the step. Each trial was then assigned to a 10-ms T_{XE} bin, and the percentage of trials with a saccade in each bin is displayed in Fig. 9*A*. Both

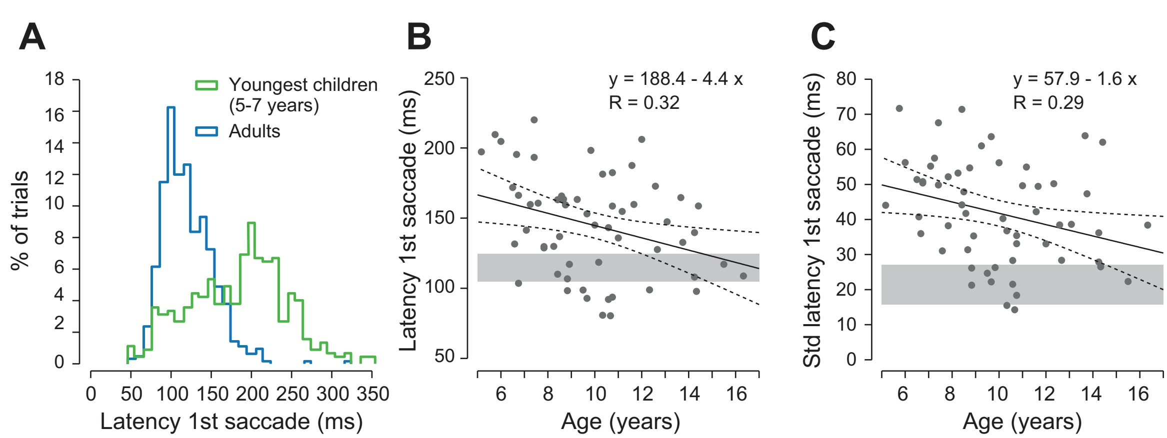

Fig. 6. *A*: histogram of the latency of the first saccade for saccadic conditions with negative VS for the youngest children and for the adults. *B* and *C*: latency of the first saccade after the steps (*B*) and standard deviation of this latency (*C*). Gray dots are the means by subjects across the 4 saccadic conditions. Regression lines show the evolution with age. Gray zones represent adult confidence intervals.

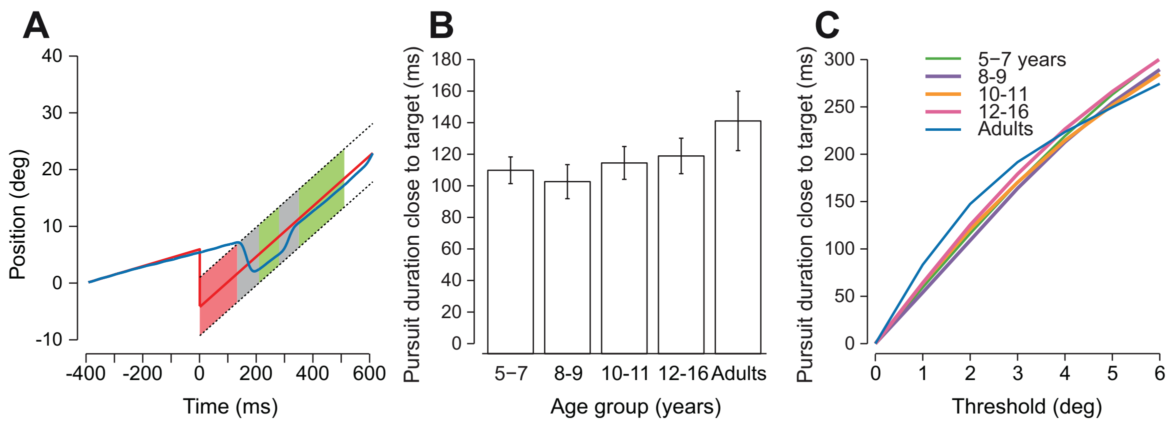

Fig. 7. *A*: pursuit duration close to the target is the sum of the duration where the position error between the eye and the target is smaller than a threshold (5°) (green parts), with the exception of the saccades (gray parts). Gaze tracking accuracy is represented by the pursuit duration close to the target. *B*: in smooth conditions, pursuit duration close to the target increases with age (close is here defined as a position error smaller than 2°). *C*: pursuit duration close to the target increases with age for a large range of thresholds.

in children and in adults, the probability of triggering a saccade is high (>60%) when there is no chance of getting to the target given current eye velocity and position ($T_{XE} < 0$). In addition, for both groups, there is a range of T_{XE} for which the probability of observing a saccade is very low (i.e., a smooth zone) as previously reported (de Brouwer et al. 2002b). The width of this smooth zone was quantified by counting the bins in which the percentage of trials with a saccade was <50%. Clearly, the duration of the smooth zone differs in adults and children (Fig. 9*A*). In other words, there is a range of T_{XE} (150–250 ms) for which adults trigger a saccade in 80% of the trials but younger children do in only 20%.

The width of the smooth zone for adults is smaller than for children aged 5–7 and 12–16 yr (permutation test: G1 vs. G5: $P = 0.02$, G2 vs. G5: $P = 0.08$, G3 vs. G5: $P = 0.20$, G4 vs. G5: $P = 0.004$). Therefore, for the same set of position and velocity errors (i.e., the same T_{XE}), adults would trigger a saccade while the youngest children would not, despite their lower pursuit performance. This indicates that adults want to catch up with the target more quickly than young children.

DISCUSSION

In the present study, we show that visually guided smooth pursuit performance improves with age until early adulthood.

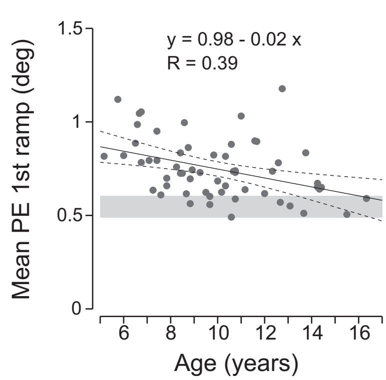

Fig. 8. Average position error (PE) on the first ramp (between 300 and 600 ms after the trial onset) decreases with age. Dots are the mean position error by subject. Evolution with age is characterized by the regression line fitted on the means by subject.

Both the average pursuit gain and acceleration increase while pursuit onset latency decreases with age. Previous studies suggest that children use a compensation strategy in order to overcome the immaturity of some functions. For instance, they rely more on visual feedback when proprioceptive feedback and state estimation are still immature (King et al. 2012). In contrast, we found that children do not execute saccades more frequently to compensate for their lower pursuit performance. Rather, they elicit fewer catch-up saccades and these saccades have longer and more variable latencies. However, these saccades are as accurate as saccades from adults. Despite the ability of children to correct for position error by accurate catch-up saccades, the low rate of saccade occurrence resulted in a larger average position error during target tracking in children compared with adults. The reduction of error correction suggests that children have a lower sensitivity to visual errors during target tracking compared with adults. We suggest that decreasing processing delays and/or better internal models with age (due to the maturation of the cerebellum) might explain the observed improvements in oculomotor behavior.

Most aspects of smooth pursuit performance improve with age until adolescence. In a previous study, Ross et al. (1993) showed that 7-yr-old children already have a mature pursuit when tracking slowly moving targets (6°/s) but not faster

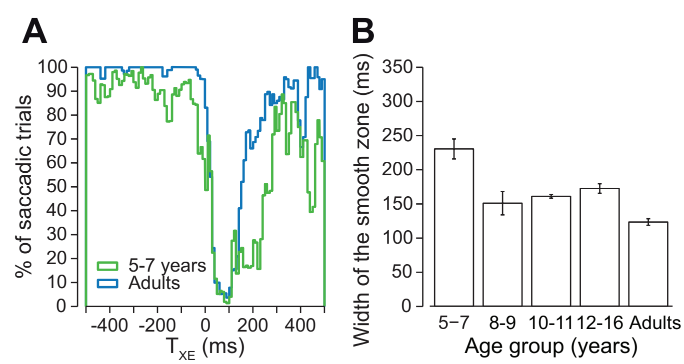

Fig. 9. Quantification of the eye crossing time (T_{XE}) leading to the execution of saccades. *A*: % of saccadic trials (with at least 1 saccade in the first 300 ms after the step) as a function of T_{XE} for the youngest children (aged 5–7 yr) and adults. T_{XE} is the time the eye will take to catch the trajectory of the target. We quantify in *B* the range of T_{XE} not leading to the execution of saccades (with a % of saccades smaller than 50%) for the different age groups.

targets (12°/s). In contrast, all the children (5–16 yr old) that participated in the present study had a mature pursuit gain for a 15°/s target. After a sudden and large change in target velocity, only children of 13 yr and older presented a mature pursuit gain. This age of maturity is similar to what was reported in other studies, although with predictable targets (Accardo et al. 1995; Katsanis et al. 1998; Salman et al. 2006b). In addition, pursuit acceleration also improved with age in the present study in response to the first and second step ramps, which contrasts with the absence of developmental changes in pursuit initiation reported previously (Ross et al. 1994). Finally, the mean and standard deviation of pursuit latency decreased with age. However, while the average pursuit latency had already reached adult level at ~8–9 yr of age, the variability of this latency remained higher than adult levels until late adolescence (~15 yr). Overall, the present results suggest that all aspects of smooth pursuit performance evolve with age and that the level of retinal slip that drives initial pursuit is an important parameter in order to investigate the limits of the smooth pursuit system.

Developmental changes in smooth pursuit reflect immaturity of motor areas of the pursuit system. In contrast with most previous studies, unpredictable target displacement was used in the present study in order to reduce the influence of predictive mechanisms on smooth pursuit performance (Barnes 2008). Therefore, pursuit parameters predominantly reflect a measure of how retinal slip is transformed into motor commands. In this transformation, retinal inputs are sent to the primary visual cortex, which relays them to the MT complex and the medial superior temporal area (MST), which are responsible for the motion processing stage as demonstrated in the monkey (Maunsell and Van Essen 1983; Newsome et al. 1988). The output of this first stage is then transformed into a motor command in order to rapidly match target velocity. This last step is located in frontal brain structures such as the frontal eye field (FEF) and in the cerebellum (monkey data: Ilg and Thier 2008; Krauzlis 2004; Lisberger 2010).

Motion processing abilities are already present in the first few months of life (Atkinson 1992; Banton and Bertenthal 1997) as assessed by visual evoked potential (VEP) (Wattam-Bell 1991) or induced optokinetic nystagmus (Banton and Bertenthal 1996). Higher-order motion processing matures later during childhood (Ellemberg et al. 2004; Klaver et al. 2008; Narasimhan and Giaschi 2012; Parrish et al. 2005), but motion perception of a simple target is probably mature much earlier. These observations are supported by the fact that motion processing areas of the extrastriate visual cortex (human homologs of MT/MST) are mature early on in the developmental time course (Burkhalter et al. 1993; Garey and de Courten 1983; Gogtay et al. 2004).

Despite presumably mature motion processing, pursuit performance was not as good in young children as in adults. These differences can be due to immaturities in motor areas of the pursuit system such as the FEF or the vermis of the cerebellum, which influence pursuit initiation as demonstrated in the monkey (FEF: Gottlieb et al. 1994; vermis: Fuchs et al. 1994; Suzuki and Keller 1988) and become mature later than the visual cortex (FEF: Bunge et al. 2002; Gogtay et al. 2004; Huttenlocher 1979; Toga et al. 2006; cerebellum: Hashimoto et al. 1995). Similarly, the cerebellar vermis plays an important role in pursuit initiation, and interesting similarities in pursuit initiation characteristics can be found between the children of our study and cerebellar patients with atrophy of midline cerebellar structures such as the vermis (Moschner et al. 1999). For instance, delayed pursuit onset, decreased initial eye acceleration, but accurate saccades to moving targets have been found in these patients as in the children of the present study. The development of the cerebellum during childhood might thus account for progressive improvement of smooth pursuit. Similarities between children and cerebellar patients have also been found in a walking adaptation task (Vasudevan et al. 2011). In this study, Vasudevan and colleagues (2011) asked children to walk on a split-belt treadmill (with 2 different speeds for the 2 legs). These authors noted that the level of adaptation of the youngest children in their study (3–5 yr old) matched that of cerebellar patients in the same task (Morton and Bastian 2006).

Children do not execute saccades more frequently to compensate for their lower pursuit performance. In adults, smooth pursuit and saccades are used in synergy to track a visual target (Orban de Xivry and Lefèvre 2007). Indeed, latency of smooth pursuit initiation, high target velocity, or sudden changes in target position or velocity can generate a large position error between the eye and the target. We could therefore hypothesize that lower pursuit in children could be compensated by more numerous and/or shorter-latency saccades that will replace the eye on the target.

A previous study by Ross et al. (1993) showed that, independently of age, children who exhibited lower pursuit performance had larger saccade amplitudes. Similarly, Accardo et al. (1995) showed that position gain of children is close to adult values despite lower velocity gain. These studies suggest that there is a good interaction between smooth pursuit and saccades in children, but no relation with age was examined. The present study demonstrates that the compensation for low pursuit performance by the saccadic system is not mature until adulthood. Indeed, children do not execute more saccades to compensate for their lower pursuit performance. Rather, they tend to delay their saccades and to perform fewer of them. In contrast, saccade programming was similar in children and in adults. That is, when a saccade was elicited it was as accurate in children as in adults.

This reduced frequency of catch-up saccades could be due to the immaturity of the saccadic system. Most developmental studies show that saccade latencies (toward stationary targets) decrease with age (Fukushima et al. 2000; Kramer et al. 2005; Luna et al. 2004) and become mature at ~12–15 yr of age. However, saccade accuracy is comparable to adults very early on (Cohen and Ross 1978; Fukushima et al. 2000; Salman et al. 2006a). Similarly, the present study demonstrates that the average latency of saccades to moving targets and the associated latency variability decrease with age. In contrast, saccadic accuracy remains comparable across all age groups. For all subjects, position error at the end of the first saccade decreases when saccadic latency increases, showing a trade-off between the time taken before executing a saccade and the movement precision. This trade-off was similar in children and adults. The amplitude of saccades to moving targets is based on a prediction of the future position error (de Brouwer et al. 2002a; Newsome et al. 1985) and therefore good motion perception ability. The similar accuracy of the catch-up saccades across age suggests that motion perception is also comparable. Children were able to execute saccades with latencies as short as adults. However, they did not trigger those short-latency saccades as often as adults. If catch-up saccades of children are accurate, why did they not compensate their low pursuit performance by increasing the frequency of those saccades?

Lower sensitivity to errors in children might result from inaccurate internal model or longer processing delays. The tendency to trigger saccades for specific combinations of position and velocity errors is assessed by a parameter called eye crossing time (T_{XE}) (de Brouwer et al. 2002b). This parameter takes into account both velocity and position errors and predicts the time horizon necessary for the eye to cross the target, hypothesizing that the eye velocity remains constant. In this study, adults did not execute saccades if the eyes were expected to cross the target between 30 and 150 ms later. This range is similar to the range found in a previous study (range between 40 and 180 ms; de Brouwer et al. 2002b). In contrast, this time interval is much longer for the youngest children (30–250 ms) but decreases with age. That is, young children have a larger tolerance to trigger catch-up saccades. This absence of correction for position errors during target tracking was also present during the first ramp for which children were on average further away from the target.

This lower sensitivity to errors in children could be explained by the immaturity of the sensory processing stage (maturation of fovea or of visual areas). However, although high-order vision continues to mature during childhood (Skoczenski and Norcia 2002), a large amount of fovea and visual area development seems to occur before the age of the youngest children studied here (Burkhalter et al. 1993; Hendrickson 1992; Yuodelis and Hendrickson 1986) and therefore does not seem to account for the reduced sensitivity to errors.

Alternatively, longer delays in the system can also decrease the rate of error correction (see Shadmehr et al. 2010b for an illustration of the phenomenon). In a manual tracking task, artificially augmenting the visual feedback delay produces a behavior that is similar to the strategy observed in children during smooth pursuit, namely, increasing visual feedback delays leads to increased tracking error (Smith 1972) and reduces the rate of corrective movements (Miall and Jackson 2006). The transition of information from motion processing areas to frontal lobes is slower in children than in adults (Paus et al. 1999). This slower transmission speed might account partially for increased pursuit and saccade latency and for the reduction of the rate of catch-up saccades. In sum, longer delays are a feature of brain immaturity (Giedd et al. 1999; Paus et al. 1999) and could account for the scarcity of catch-up saccades in young children.

To overcome these delays, humans use predictions of the consequences of their movements (by internal models) to monitor their performance (Shadmehr et al. 2010b). Immature and unreliable internal models in children could postpone corrections because of unreliable predictions. Hence, the cerebellum, which is a key neural substrate of internal models (Blakemore et al. 1998; Izawa et al. 2012), is also a central component for error detection and correction during visually guided smooth pursuit (Medina and Lisberger 2008; Stone and Lisberger 1990) as it is in other contexts (Diedrichsen et al. 2005; Fiez et al. 1992). The lower error correction during ongoing smooth pursuit eye movements could therefore be due to the late maturity of the cerebellum (Castellanos and Lee 2002; Hashimoto et al. 1995; Tiemeier et al. 2010).

In summary, the results obtained in the present study suggest that, from childhood through midadolescence, maturation of brain areas such as the cerebellum and increase in transmission speed shape oculomotor behavior.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: C.E., J.-J.O.d.X., M.-C.N., D.Y., and P.L. conception and design of research; C.E. performed experiments; C.E. and J.-J.O.d.X. analyzed data; C.E., J.-J.O.d.X., M.-C.N., D.Y., and P.L. interpreted results of experiments; C.E. prepared figures; C.E. and J.-J.O.d.X. drafted manuscript; C.E., J.-J.O.d.X., M.-C.N., D.Y., and P.L. edited and revised manuscript; C.E., J.-J.O.d.X., M.-C.N., D.Y., and P.L. approved final version of manuscript.

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